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A MORPHOMETRIC ANALYSIS OF THE *LEPTOSIPHON ANDROSACEUS* COMPLEX (POLEMONIACEAE) IN THE CENTRAL AND SOUTH COAST RANGES

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Abstract

The taxonomy of the *Leptosiphon androsaceus* Benth. complex has been troublesome because of remarkable morphological similarity among species. During the past 160 years, members of this complex have been classified in 4 different genera, and numerous specific and infraspecific names have been applied. Despite numerous treatments written by early taxonomists, analytical studies were not performed on these species until recently. We examined morphometric relationships among 1264 individuals from 51 populations, from the Central and South Coast Ranges. We focused on populations from San Francisco to Santa Barbara County because much of the variability in flower color occurs in this region, and color has been used by previous authors to distinguish species and subspecies. We investigated morphological variation using an array of multivariate analyses, including cluster analysis, principal components analysis, and discriminant analysis. Our analyses show six species of the *L. androsaceus* complex occur in this region of California: *L. acicularis* (Greene) Jeps., *L. androsaceus, L. bicolor* Nutt., *L. croceus* (Eastw.) J. M. Porter & L. A. Johnson, *L. parviflorus* Benth., and *L. rosaceus. Leptosiphon croceus* and *L. rosaceus* were described nearly 100 years ago, but have not been included in recent treatments. Our results offer strong support for recognition of *L. croceus* and *L. rosaceus* at the species level.

The *Leptosiphon* (=*Linanthus*; see below) *androsaceus* group is a monophyletic lineage of Polemoniaceae (Bell and Patterson 2000) characterized morphologically within the genus by sessile flowers borne in terminal, bracteate heads, salverform corollas with long filiform tubes, and calyces with narrow intercostal hyaline membranes connecting the lobes. Although visited and presumably pollinated primarily by long-tongued flies, the species within the *L. androsaceus* complex exhibit a variety of breeding systems (Goodwillie 1997, 1999a, b).

Within the salverform-tubed leptosiphons, relative breadth of calyx membranes and lobes distinguishes two well marked groups (Table 1): the *L. androsaceus* group, characterized by membranes clearly narrower than the lobes, and the *L. ciliatus* group with membranes broader than the lobes. This distinction is also supported by molecular data (Bell and Patterson 2000). All are small, spring-blooming annuals occurring in grassland and woodland areas from the Sierra Nevada foothills to the Pacific Coast in western North America.

The remarkable morphological similarity among these species has hampered resolution of species limits and relationships. Furthermore, the nomenclature is extensive (Jepson 1943; Mason 1951; Munz 1959) and the task of sorting and assigning names is challenging. Hooker (1870) referred to *Linanthus* as "one of the most variable genera of hardy annuals, the limits between the species of which are as difficult to draw from living specimens as from herbarium ones." There are few morphological characters available to distinguish these similar species, and compounding the taxonomic confusion is the fact that these characters often exhibit a high degree of variability within a species. *Leptosiphon parviflorus,* for example, is an especially variable species with regard to corolla tube length and corolla color, two characteristics traditionally used to identify species.

Taxonomic background. In his monograph of Polemoniaceae, Grant (1959) recognized 6 sections of *Linanthus* based on several morphological features. Among these was his sect. *Leptosiphon.* The earliest recognized species in this section were described originally by Bentham (1833) as members of the genus *Leptosiphon.* Greene (1889–1892) combined several genera into a single genus, *Linanthus,* based largely on the presence of opposite, palmately lobed leaves. Grant's (1959) sections largely represent the genera that were combined into *Linanthus* by Greene. Porter and Johnson (2000) presented a revision of the entire family with the goal of recognizing only monophyletic groups. Their revision, supported by morphological and molecular data (Johnson et al. 1996; Porter 1996; Bell et al. 1999; Bell and Patterson 2000) divides *Linanthus sensu* Greene into two distinct, non-sister genera, *Linanthus* and *Leptosiphon;* the latter genus includes, but is not limited to, all of the *L. androsaceus* group. We follow Porter and Johnson's taxonomy in this paper (Table 1).

Although many treatments involving the *L. androsaceus* group have been provided by earlier taxonomists (Bentham 1833, 1845, 1849; Endlicher 1836–1840; Nuttall 1848; Bentham and Hooker 1876; Gray 1870, 1886; Greene 1889–1892; Jepson 1901, 1925, 1943; Danforth 1945; Mason 1951), no

Table 1. Taxonomy of Long-Tubed *Leptosiphon*.

L. ciliatus group—calyx membranes wider than calyx lobes
L. breviculus (A. Gray) J. M. Porter & L. A. Johnson
L. ciliatus (Benth.) Jeps.
L. montanus (Greene) J. M. Porter & L. A. Johnson
L. nudatus (Greene) J. M. Porter & L. A. Johnson
L. oblanceolatus (Brand) J. M. Porter & L. A. Johnson
L. androsaceus group—calyx membranes narrower than calyx lobes
L. acicularis (Greene) Jeps.
L. androsaceus Benth.
L. bicolor Nutt.
L. croceus (Eastw.) J. M. Porter & L. A. Johnson
L. jepsonii (Schemske and Goodwillie) J. M. Porter & L. A. Johnson
L. latisectus (E. G. Buxton) J. M. Porter & L. A. Johnson
L. minimus (H. Mason) R. Battaglia
L. parviflorus Benth.
L. rosaceus (Greene) R. Battaglia
L. serrulatus (Greene) J. M. Porter & L. A. Johnson
unidentified populations
MRM Morgan Meadow, Santa Cruz Co.
PIN Pinnacles National Monument, San Benito Co.

analytical studies have been performed. The first explicit analyses include two recent morphometric studies that sampled populations in northern California where the distribution ranges of these taxa overlap (Buxton 1993; Schemske and Goodwille 1996). Each of these studies revealed the presence of previously unrecognized taxa and provided statistical support for the recognition of the other members of this complex. Nevertheless, these studies sampled only a fragment of the variation present in the entire complex.

Only through quantitative data analyses can species limits within the complex be resolved. Determination of species limits is a prerequisite for understanding phylogenetic relationships among members of this group. Our study continues to clarify taxonomic relationships in the *L. androsaceus* complex by sampling from populations in the southern portions of its range. In order to determine which taxa occur in this geographic area, we used a number of multivariate analyses (PCA, Cluster, DA) to group specimens based on morphological similarities. We were specifically interested in determining whether any of the various *L. parviflorus* color morphs merited taxonomic recognition. Once the taxonomic groups were identified, we used PCA and DA analyses to identify the morphological characteristics most responsible for distinguishing the taxa.

Methods

Sampling. Quantitative morphological data for this study were gathered from fresh specimens collected during spring of 1997 and 1998. We collected 1264 samples (individual plants) from 51 populations from San Francisco to Santa Barbara County (Table 2; Fig. 1). This is the region in which *L. parviflorus,* a particularly troublesome taxon, exhibits the greatest variation in color and color pattern.

In addition, plants were grown in the greenhouse from field-collected seed to estimate whether observed character differences were influenced by environmental conditions. Cotyledon measurements were also made on these plants.

Characters. We obtained a range of leaf and floral measurements and observations to represent the overall form of the plant (Table 3). A total of 44 measurements was taken on each specimen. Many of these characters have been used to distinguish among species in this complex. To ensure that measurements were comparable, specimens for measurements were prepared as follows: From each plant, one leaf and one flower were mounted on an overhead transparency using clear packing tape. The first leaf below the inflorescence was chosen to represent the leaves of the plant. The calyx and corolla were dissected prior to being examined. The calyx was cut between the lobes to flatten it and obtain a clear image. The corolla was dissected by peeling three or four of the limb lobes, including the throat, from the tube and mounting them independently. The stigmas and style were removed and mounted.

Measurement. Qualitative characters, counts, and two length measurements were scored by hand prior to mounting specimens. Schemske and Goodwillie (1996) showed patterns of calyx pubescence in this group fall into two categories; fewer than 100 or greater than 100 trichomes per lobe. We counted the number of trichomes per calyx lobe if they numbered fewer than 100.

The remaining continuous characters were measured by digitizing the contours of the mounted specimens using a computerized image capturing system. We used the software program MorphoSys ver. 1.26 (Meacham and Duncan 1989), which allows the contour of a specimen to be drawn, landmarks selected, and data saved. This allowed for a relatively rapid and accurate means of collecting the large amount of data necessary for a morphometric analysis. Width measurements for the corolla and leaf lobes were spaced proportionally throughout the proximal region of the lobe, at 0.5, 0.7, 0.8, and 0.9 of the total length of the lobe, because this region appeared to be the most variable.

Analytical techniques. We used several multivariate methods per Pimentel's (1993) recommendation. If the results of several different analyses agree, then violations of assumptions such as nonlinearity and heteroscedacity are minimized and the results of the analyses are robust. The multivariate statistical methods we used included: Cluster Anal-

TABLE 2. COLLECTION LOCALITIES OF *LEPTOSIPHON* SAMPLES. All collections were made in 1998 except EDG, MPT, MTH, PIN, RSA, and WSK, which were made in 1997. See Table 4 for color code translation.

Acronym	Location	Number sampled (N)	Color code
L. acicularis			
BFX	Bolinas Fairfax Rd., Marin Co.	14	9
PLR	Pleasanton Ridge Regional Park, Alameda Co.	25	9
SNB	Sinbad Canyon, Pleasanton Ridge Regional Park, Alameda Co.	25	9
L. androsaceus			
AQS	Almaden Quicksilver County Park, Santa Clara Co.	25	10
BFR	Bolinas Fairfax Rd., Marin Co.	25	10
BNK	Bunker Hill, Highway 280, San Mateo Co.	25	10
DUN	East Dunne Rd., Santa Clara Co.	25	10
JPR	Jasper Ridge Biological Preserve, San Mateo Co.	25	10
LMP	Reynolds Rd., Stanton Ranch, Santa Clara Co.	25	10
MHM	Eastern side of Mount Hamilton, Santa Clara Co.	25	10
MIN	Mines Rd., Alameda Co.	25	10
MTD	Mount Diablo State Park, Contra Costa Co.	25	10
MTH	Mt. Hamilton, Santa Clara Co.	24	10
RSA	Rancho San Antonio County Park, Santa Clara Co.	15	10
RSN	Rancho San Antonio County Park, Santa Clara Co.	25	10
UVA	Uvas Rd., Santa Clara Co.	25	10
L. bicolor			
ADL	Paso Robles, San Luis Obispo Co.	25	11
CHI	Red Hill Rd., Chinese Camp, Tuolumne Co.	25	3
COL	Coalinga Road, Monterey Co.	25	11
DPC	Del Puerto Canyon Rd., Santa Clara Co.	25	3
PRB	Parkfield, Monterey Co.	25	11
RDH	Red Hill Rd., Chinese Camp, Tuolumne Co.	25	11
STR	Reynolds Rd., Stanton Ranch, Santa Clara Co.	25	11
VNY	Vineyard Canyon Rd., Monterey Co.	25	3
WSK	Whiskey Falls, Madera Co.	22	11
L. croceus			
MSB	Moss Beach, San Mateo Co.	25	8
L. latisectus			
CUT	Potter Valley, Mendocino Co.	25	11
EEL	Potter Valley, Mendocino Co.	25	11
P. parviflorus			
ALQ	Almaden Quicksilver County Park, Santa Clara Co.	25	1
CAC	Cachagua Rd., Monterey Co.	25	1
CLG	Coalinga Rd., Monterey Co.	25	3
CRZ	Highway 58, San Luis Obispo Co.	25	2
CVR	Carmel Valley Road, Monterey Co.	25	2
DLP	Del Puerto Canyon Rd., Santa Clara Co.	25	3
DNN	East Dunne Rd., Santa Clara Co.	25	1
EDG	Edgewood County Park, San Mateo Co.	24	1
EGW	Edgewood County Park, San Mateo Co.	25	1
EHT	Carmel Valley Road, Monterey Co.	25	2
FGM	Figueroa Mountain Rd., Santa Barbara Co.	25	2
FGS	Happy Canyon Rd., Santa Barbara Co.	25	2
FIG	Figueroa Mountain Rd., Santa Barbara Co.	25	2
FTO	Impossible Canyon, Fort Ord, Monterey Co.	25	6
HST	Hastings Natural History Reservation, Monterey Co.	25	4
JSP	Jasper Ridge Biological Preserve, San Mateo Co.	25	1
JSR	Jasper Ridge Biological Preserve, San Mateo Co.	25	5
LPD	Los Padres National Forest, San Luis Obispo Co.	25	6
LCU	Lucile's Court, Boulder Creek, Santa Cruz Co.	25	8
PKS	Parkfield, Monterey Co.	25	2
PNC	Pinnacles National Monument, San Benito Co.	25	3
PRK	Parkfield, Monterey Co.	25	6
QHL	Quail Hollow Ranch County Park, Santa Cruz Co.	25	7

TABLE 2. CONTINUED

Acronym	Location	Number sampled (N)	Color code
SAZ	Near Sierra Azul County Park, Santa Clara Co.	25	1
SND	Sandhill Rd., Santa Cruz Co.	25	2
TRK	Turkey Flat Campground, San Luis Obispo Co.	25	6
L. rosaceus			
MPT	Mori Point, San Mateo Co.	24	3
MRI	Mori Point, San Mateo Co.	25	3
unidentified			
MRM	Morgan Meadow, Santa Cruz Co.	25	10
PIN	Pinnacles National Monument, San Benito Co.	9	2
PNN	Pinnacles National Monument, San Benito Co.	25	2

ysis of a dissimilarity matrix (UPGMA), Principal Components Analysis (PCA) using a correlation matrix of the standardized data sets, and Discriminant Analysis (DA) on a variance-covariance matrix.

Several data matrices were used in our analyses. A summary of each data matrix with regard to identity, number of groups, number of specimens, and number of variables is shown in Table 4. Matrices 1, 2, and 2a were used to determine how many taxa (species) occured in the study region. Matrix 1 contains all data collected from field specimens during spring and summer 1998, and was used for screening variables to be included in the final analyses. Matrix 2 is a subset of Matrix 1 resulting from data evaluation, and containing representative samples from all species in the *L. androsaceus* complex except for *L. jepsonii, L. minimus* and *L. serrulatus* (Greene) J. M. Porter & L. A. Johnson comb. nov. These species do not occur in the geographical range covered by this study.

Matrices 3 and 4 were used to evaluate whether *L. parviflorus* color morphs merited infraspecific recognition. Matrix 3 is a subset of Matrix 1, containing representative samples from only populations identified as *L. parviflorus* and the *L. croceus* population from Moss Beach (MSB). *Leptosiphon croceus* was included in this data set to assess its relationship to *L. parviflorus.* It is the final data set for *L. parviflorus* resulting from data evaluation. Matrix 4 contains only populations identified as *L. parviflorus,* and was used to determine whether any of the various color morphs deserved taxonomic recognition.

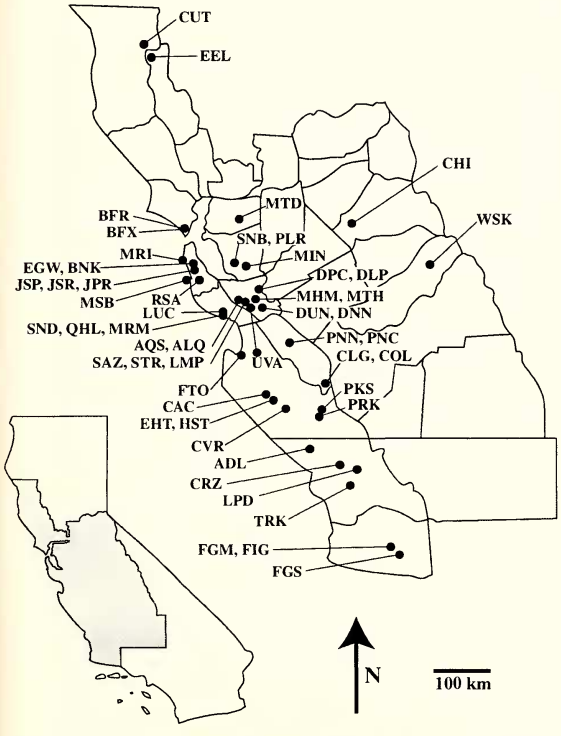

FIG. 1. Location of *Leptosiphon* samples included in this study.

Data evaluation. Multivariate techniques require a rigorous examination of data, because the effects of an ill-conditioned data set can be compounded across several variables and have quite substantial effects (Tabachnick and Fidell 1996). To minimize these risks, data from Matrix 1 were screened for accuracy, precision, missing data, and co-linearity. Several qualitative variables were excluded due to either difficulty in consistent interpretation of character ranks or a high degree of variability observed within a single population. These include calyx trichome length, corolla tube pubescence and glandularity, corolla throat pubescence, leaf pubescence and glandularity, degree of branching, conivent versus spreading stamens, number of bracts, number of internodes, and number of open flowers.

Because corolla color and color pattern were consistent within populations, the variables for tube, abaxial lobe, adaxial lobe, and throat ring color were summarized into one variable describing the 11 different color morphs (Table 5) observed in this study. These data were used only in the anal-

TABLE 3. MORPHOLOGICAL CHARACTERS ANALYZED. All distance measurements are in mm.

	Qualitative	MorphoSys	Hand-scored	Used in multivariate analysis
Calyx:				
Length of lobes		X		X
Total length of calyx		X		X
Width of calyx lobe:				
at 0.5 length of lobe		X		X
at base of lobe		X		X
Location of calyx pubescence (absent/ciliate/throughout)	X		X	
Degree of calyx pubescence (# trichomes/lobe)			X	Matrix 2
Length of calyx trichomes (short/medium/long)	X		X	
Glandular/not glandular	X		X	
Corolla:				
Length of corolla lobe		X		X
Width of corolla lobe:				
at base		X		
at 1/10 from lobe base				
at 5/10 from lobe base		X		X
at 7/10 from lobe base		X		
at 8/10 from lobe base		X		
at 9/10 from lobe base		X		X
Length of throat		X		X
Length of tube		X		X
Width of tube		X		X
Tube color	X		X	
Tube pubescence (absent/sparse/dense)	X		X	
Tube trichomes glandular/not glandular	X		X	
Throat trichomes present/absent	X		X	
Lobe color:				
Abaxial surface	X		X	
Adaxial surface	X		X	
Throat ring color	X		X	
Androecium and gynoecium:				
Length of filament		X	X	
Length of stigma			X	Matrix 2
Length of style			X	
Leaf:				
Length of palm		X		X
Width of palm		X		X
Length of middle lobe		X		X
Width of middle lobe:				
at base of lobe		X		X
at ½ from lobe base		X		X
at ¼ from lobe base		X		Matrix 3 & 4
at ⅛ from lobe base		X		X
Number of lobes per leaf			X	X
Pubescence (absent/ciliate/throughout)	X		X	
Glandularity (present/absent)	X		X	
General:				
Number of internodes on longest stem			X	
Number of open flowers per inflorescence			X	
Number of bracts subtending inflorescence			X	
Branching (none/above/below/throughout)	X		X	
Stamens connivent/spreading	X		X	
Total height of plant			X	X

TABLE 4. DATA MATRICES USED IN ANALYSES. The number of groups refers to the number of groups used for multivariate analyses. Matrices 5–8 were not used in the multivariate analyses.

Data matrix	Description	Groups in analysis	Populations represented	Number of specimens	Number of variables
Matrix 1	All 1998 field data	53	53	1314	44
Matrix 2	Results of data analysis, all species included	51 (DA2-1) 9 (DA2-2)	51	1264	21
Matrix 2a	Variable means for each population in Matrix 2	1	51	51	21
Matrix 3	Results of data analysis, only *L. croceus* and *L. parviflorus* populations included	26	26	650	20
Matrix 3a	Variable means for each population in Matrix 3	1	26	26	20
Matrix 4	Results of data analysis, only *L. parviflorus* populations included	25 (DA4-1) 7 (DA4-2)	25	625	20
Matrix 5	All field data from 1997	N/A	6	118	29
Matrix 6	1997 Greenhouse data	N/A	3	72	26
Matrix 7	1998 Greenhouse data	N/A	19	276	26
Matrix 8	Cotyledon data from 1998 greenhouse plants	N/A	19	447	2

ysis involving populations of *L. parviflorus*. Most species in the *L. androsaceus* complex have two color morphs: white, and either pink, lavender, or yellow. *Leptosiphon parviflorus* is unique in that all the above color morphs occur. In addition, throat color varies, and markings on the limb lobes may be present (Fig. 2). Eight different color morphs of *L. parviflorus* were observed in this study.

Measurements taken using MorphoSys were first checked for precision (repeatability) by randomly choosing one population and remeasuring for each variable. Measurements that showed significant differences ($P > 0.05$) between measurement sessions were eliminated from our analysis.

The remaining 27 variables (23 metric continuous, two metric counts, one multistate, and one binary) were then checked for near-perfect correlation to reduce the risk of co-linearity. Multi-co-linearity problems occur when $r > 0.9$ (Tabachnick and Fidell 1996); therefore we eliminated selected variables from pairs with Pearson's correlation scores of $r > 0.9$.

Calyx pubescence and glandularity posed problems with data scoring. Degree of calyx pubescence could be measured as number of trichomes per lobe, but the trichome location and glandularity had to be coded (multistate and binary respectively). However, all three characters were highly correlated (all r values > 0.92), thus the two coded variables were omitted.

Style exsertion has been used in the past (Bentham 1833; Greene 1889–1892; Mason 1951; Munz 1959; Buxton 1993) to aid in characterizing members of this complex. We observed that style length, and therefore style exsertion, increased with age of the flower in *L. parviflorus*. In addition, tube length and style length were highly correlated, $r = 0.944$. Despite its previous taxonomic use, we excluded style length from our analysis.

Statistics. Cluster analysis was used to suggest similarity among populations. Results from the cluster analyses allowed us to define groups in later analyses that require group identity. Population

TABLE 5. COROLLA COLOR PATTERNS RECORDED IN THE *LEPTOSIPHON ANDROSACEUS* COMPLEX.

Color code	Lobe color	Throat color	Additional markings
1	white	yellow	2 red spots at base of lobes ("two-spot")
2	white and/or lavender-pink	violet or yellow	striations on lobes ("candystripe")
3	white	yellow	
4	white	violet	
5	pink	yellow	2 red spots at base of lobes ("two-spot")
6	white	orange	1 red bar at base of lobes ("bullseye")
7	deep yellow-orange	orange	
8	deep yellow-orange	orange	2 red spots at base of lobes ("two-spot")
9	light buttery yellow	light yellow	
10	white or lavender-blue	violet at base, yellow distally	
11	pink	yellow with white ring distally	

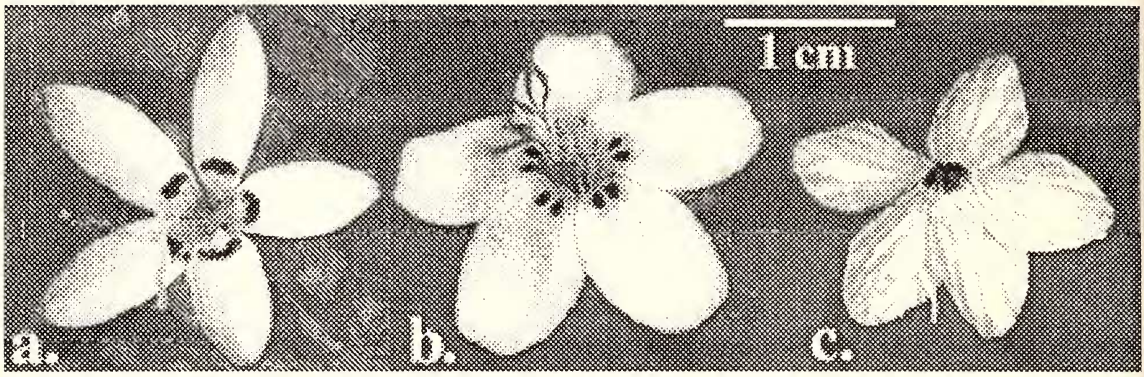

FIG. 2. Examples of the various corolla markings observed in *L. parviflorus:* a) "bullseye", red crescent shaped bar at base of lobe, b) "2-spot", two red spots at base of lobe, c) "candystripe", lavender striations on lobe.

means (group centroids) for each variable in Matrix 2 and Matrix 3 were calculated. New data matrices (Matrix 2a and Matrix 3a) were created using variable means for each population, and each was subjected to cluster analysis. The group average method for linkage (UPGMA) using a dissimilarity matrix generated by Euclidean distances was used (Sneath and Sokal 1973).

Principal components analysis (PCA) was primarily used to analyze the variables on a correlation matrix of the data sets Matrix 2 and Matrix 3. Data were standardized prior to the analysis as part of the SPSS (SPSS 1997) protocol for the PCA method.

Discriminant analysis (DA) was performed on a variance-covariance matrix of the Matrix 2 and Matrix 4 data sets. Discriminant analyses were run on the two data sets using several a priori grouping arrangements. Three analyses (DA2-1, DA2-2, DA2-3) were run on Matrix 2. DA2-1 used the 51 collection populations as predefined groups. DA2-2 used the results from the UPGMA and PCA analyses to assign individuals to the following groups: PNN, MRM, *L. androsaceus, L. acicularis, L. bicolor, L. latisectus, L. parviflorus, L. croceus,* and *L. rosaceus.* Because the sizes of the groups in DA2-2 were not equal (ranging from 25 to 625 individuals per group), the analysis was repeated using equal group sizes. DA2-3 used a subset of 25 individuals selected randomly from each group used in DA2-2. The Matrix 4 data set was subjected to two DA analyses, DA4-1 and DA4-2. A priori groups were defined by color morphology and based on the results from the PCA and cluster analyses: "2-spot" (all corolla colors), "bullseye," "candystripe," "yellow," "white with violet," and "white with yellow." The sizes of the groups based on color morphology were not equal, ranging from 25 to 200 individuals. The same reduction procedure was performed by randomly selecting 25 individuals from each group, and the analysis was run again (DA4-2).

RESULTS

Because of their large size, matrices generated (correlation, component, structure) and Geisser classification summaries are not included in this paper, but are in Battaglia (1999) or are available from the first author upon request. Results of analyses using all species are discussed first, results from the *L. parviflorus* color morph analyses are discussed second. Four of the 51 populations (MRI, MSB, PNN, MRM) were not identifiable using the current taxonomy (Patterson 1993; Buxton 1994; Schemske and Goodwillie 1996). Two of these were later identified as *L. croceus* (MSB) and *L. rosaceus* (MRI), species synonomized with *L. parviflorus* and *L. androsaceus* respectively. The PNN and MRM populations remained unidentifiable.

Cluster analysis—all species. The UPGMA cluster analysis of Matrix 2a (Fig. 3) is in general accord with the conventional taxonomy of the group, with several noteworthy exceptions. Five of seven species cluster together; however, *L. acicularis* and *L. parviflorus* do not.

Principal components analysis—all species. Results of PCA on Matrix 2 showed the total variance was generally well spread among variables, with only 77% of the total variance explained by the first 6 components. This indicates variables were generally independent of each other, with little correlation or covariation. Graphical representation of regression factor scores for each individual (not shown) indicate seven distinct clusters representing *L. acicularis, L. androsaceus, L. rosaceus, L. croceus, L. parviflorus, L. latisectus,* and *L. bicolor.*

Results from the component matrix indicate there was no single variable contributing to the observed variation among groups. More interestingly, corolla tube length had component scores of 0.232, −0.008, and 0.203 for the first three components. This indicates corolla tube length explained little of the observed variation. Although corolla tube length is traditionally used as a character to distin-

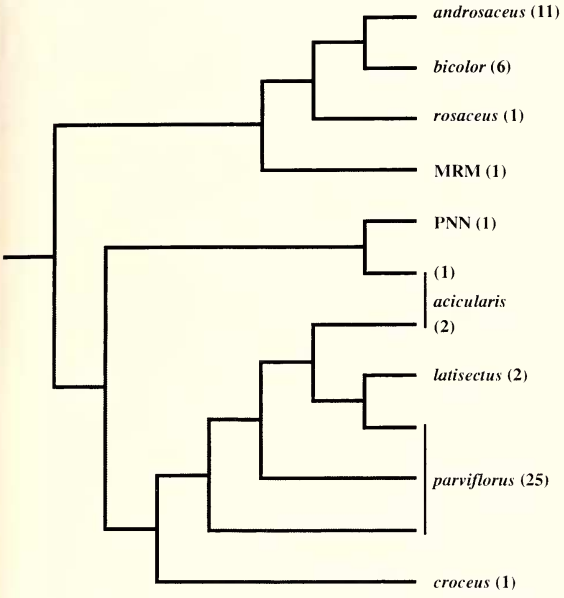

FIG. 3. Dendrogram of UPGMA cluster analysis for all species (Matrix 2a). MRM (Morgan Meadow) and PNN (Pinnacles) are two unidentifiable populations. Numbers in parentheses refer to the number of populations represented by the branch.

guish among species in this complex, it does not correlate with segregation on the first three components.

Discriminant function analysis—all species. (DA2-1). When using a priori groups based on the 51 collection sites, all Wilks' Λ values were small (0.040–0.575), indicating strong differences among group centroids for each variable. ANOVA's show significant differences ($P < 0.001$) among all variable means for each of the 51 populations.

Results of the Geisser classification summary for the 51 collection sites indicate three populations have 100% classification success: MSB (*L. croceus*), CHI (*L. bicolor*), and LUC (*L. parviflorus*). Ten populations have greater than 90% classification success: AQS, RSN, UVA (*L. androsaceus*), COL, STR (*L. bicolor*), CLG, JSR, QHL (*L. parviflorus*), MRI (*L. rosaceus*), and PNN (undetermined). One group, TRK (*L. parviflorus*), has a low score of 54%, and the remaining groups range from 64–88%. Of the 1264 individuals, 1053 (83.3%) were classified correctly based on collection site, indicating that all groups are unique.

Misallocations to collection sites in geographical proximity occurred frequently. In nearly every case, misallocations were within species groups that resulted from the UPGMA and PCA analyses. The exceptions involve three of the four unusual populations identified in the previous analyses. MRI (*L. rosaceus*) had 24 correct hits and 1 misallocation to BFR (*L. androsaceus*); PNN had 24 correct hits and 1 misallocation to ADL (*L. bicolor*); and MRM had 16 correct hits, 4 incorrect classifications to JSR and CAC (*L. parviflorus*) and 5 misallocations to RSN (*L. androsaceus*). The unusual population from MRM was the only one to have members classified into two other species groups.

Results from DA2-3 (a priori groups of equal numbers defined by UPGMA and PCA, respectively) appear below. We do not discuss in detail results from DA2-2 because general patterns regarding group discrimination were the same, and graphical interpretation in two dimensions is complicated with the larger sample size. In each case one-way ANOVAS indicated variable means for all groups differed significantly ($P < 0.001$).

The first three canonical functions contained 74.4% of the variation in DA2-3, and the variance was evenly distributed among the functions. The first function in DA2-3 contained 33.3% of the variation. Strong group differences for all variables in DA2-3 was indicated by generally low Wilks' Λ scores (0.168–0.674). The majority of variables scored lower than 0.5.

Patterns are revealed by graphing the first two canonical discriminant functions (Fig. 4). Group separation is distinct: *L. croceus* and *L. rosaceus* are clearly separated from *L. parviflorus* and *L. androsaceus* respectively, *L. bicolor* and PNN are not separated, and MRM is closely associated with *L. androsaceus,* although individuals are still scattered between *L. parviflorus* and *L. androsaceus.*

A three-dimensional depiction (Fig. 5) of the first three discriminant function scores for individuals in DA2-3 reveals 7 distinct clusters, each corresponding to one of the 7 species. Individuals from the PNN and MRM populations do not form coherent groups.

Geisser classification results for each analysis are similar. In DA2-2 all but MRM (76%) have above 90% successful predicted group membership. In DA2-3, all but *L. androsaceus* (94%) have 100% successful classification.

Cluster analysis—L. parviflorus *color morphs.* We performed a UPGMA cluster analysis on the Matrix 3a data set to evaluate support for grouping *L. parviflorus* populations based on corolla color pattern (Fig. 6). *Leptosiphon croceus* (MSB) is clearly separated from *L. parviflorus.* Within *L. parviflorus,* all but one of these populations displaying two spots at the base of the petal lobe cluster together. Three populations with the "bullseye" pattern form a cluster, but this cluster and the excluded population LPD are nested deeply within the remaining populations of *L. parviflorus.* No other color morphs form discrete clusters.

Discriminant analysis—L. parviflorus *color morphs.* We performed a DA on the Matrix 3a data set. Based on the results of the previous analyses, all of the "2-spot" color morphs (white or pink) were grouped together for this analysis. The results from DA4-1 and DA4-2 were nearly identical, in-

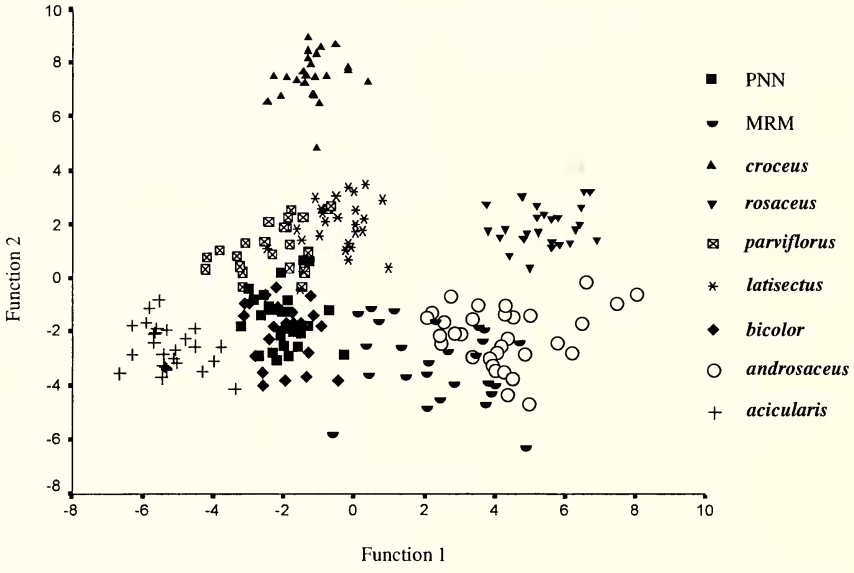

FIG. 4. Discriminant analysis results from all species (Matrix 2), equal group sizes (DA2-3). Graph of first two canonical functions for each individual.

dicating the unequal group sizes within DA4-1 did not adversely affect the analysis. Only the results from DA4-1 (all *L. parviflorus* individuals) will be discussed.

Wilks' Λ values for the variables were mostly greater than 0.8, demonstrating weak differences among group centroids for each variable; however, ANOVAS revealed that variable means for all groups were significantly different ($P < 0.001$). Tube length was the only variable for which there was a strong group difference (Wilks' $\Lambda = 0.385$). The three petal lobe measurements (tube width, plant height, and leaf mid-lobe width) had Wilks' Λ scores ranging from 0.518 to 0.673.

Geisser classification showed that "candystripe" morphs had the lowest predicted group membership scores, with 71% being classified correctly. Misallocations for this color morph were made to each other color group, with the greatest number (25) being classified into the "white with violet" group.

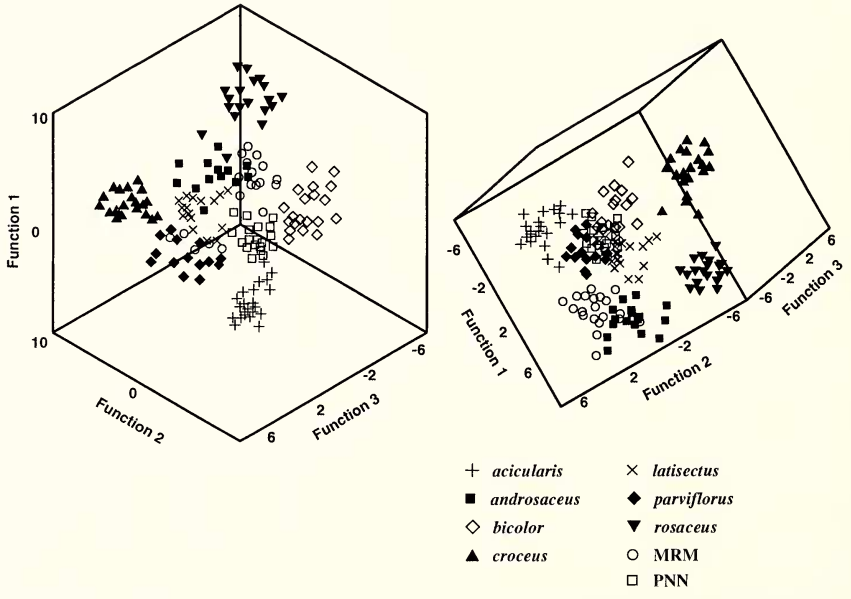

FIG. 5. Discriminant analysis results from all species (Matrix 2), equal group sizes (DA2-3). a) Three dimensional graph of the first three discriminant scores for each individual. b) Same graph with axes rotated.

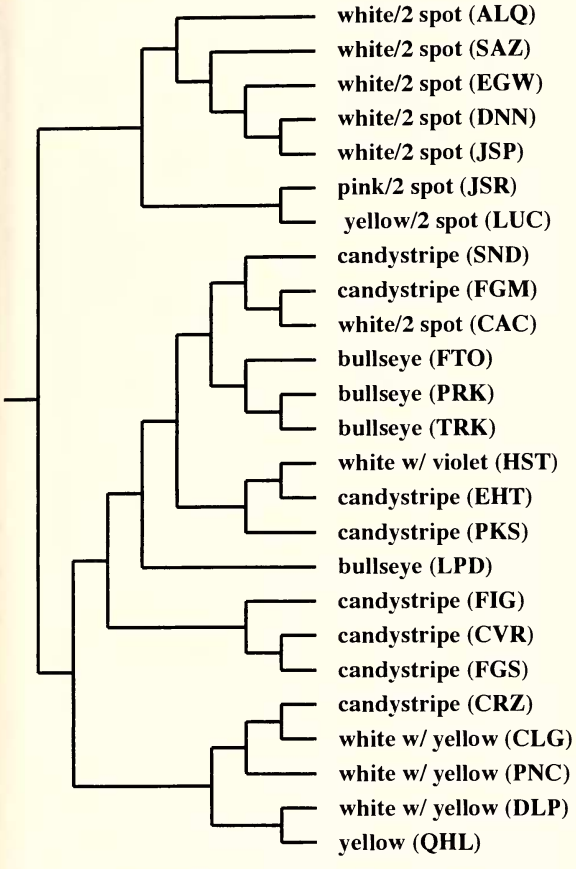

FIG. 6. Dendrogram of UPGMA cluster analysis for *L. parviflorus* color morphs (Matrix 3a). Acronyms refer to population locations.

The "white with violet" flowers were allocated correctly 92% of the time; however these specimens came from one population, and the two misclassified individuals were allocated to the "candystripe" group.

The "2-spot" morphs had 87.5% correct classification, which was lower than expected based on results from PCA but consistent with prior PCA and cluster analyses. Of 200 specimens, 175 were classified correctly and 25 were misallocated to each of the other color morphs. Case-wise examination of these 25 misallocations showed 22 were from the CAC population, the same population that did not cluster with other "2-spot" populations in the cluster analysis. Taking this into consideration, the remaining individuals of the "2-spot" morph show 98% correct classification.

The "white with yellow" and the "yellow" morphs had high classification rates, 97.3% and 100% respectively. The two misallocations of the "white with yellow" morph were to the "yellow group," a single population. The "white with yellow" morph shows general affinity for the "yellow" morph based on misallocations, but with 100% classification of "yellow," affinities of "yellow" with other morphs cannot be assessed.

The correctly predicted group membership for "bullseye" was 86%, but no affinities to other groups could be determined because misclassified individuals were allocated to each of the other color morphs. In addition, misallocations did not share similar patterns observed in the PCA and cluster analyses. In the UPGMA tree, FTO, TRK, and PRK clustered together, while LPD was excluded. Case-wise analysis of the misallocations revealed nine of 14 misallocations were from the FTO population, rather than the LPD population. Results from discriminant analysis are consistent with geographical distributions of these populations: FTO occurs near the coast while PRK, TRK and LPD are closer to each other in the inner Coast Ranges.

We extracted five canonical discriminant functions in our analysis; 93% of the total variation was explained in the first three axes (55.7%, 24.5%, and 12.8%, respectively). Corolla tube length and width scored high on the first axis (0.677 and 0.494). Corolla tube length is not particularly informative in distinguishing species in the Matrix 2 analyses, but it is important in distinguishing the "2-spot" *L. parviflorus* morphs from the remaining color morphs. Width of corolla lobe at the tip contributes most to the second axis, separating the narrower lobed "bullseye" morphs from the more rounded "white with yellow" morphs (Fig. 7).

Group differences based on individual variables. Results from the PCA and DA demonstrated that most variables were necessary for distinguishing among groups, whether they were groups based on species or color morphs of *L. parviflorus*. Discrimination among species was primarily based on calyx pubescence, corolla lobe length, corolla lobe width, and leaf lobe width. When only *L. parviflorus* populations were examined, PCA indicated most all variables were necessary for discrimination. On the other hand, DA showed corolla tube length and width, along with corolla lobe tip width, to be the most important variables in distinguishing the "2-spot" morphs from the remaining color morphs of *L. parviflorus*.

Greenhouse data. Nearly all measurements (means for each variable) from the plants grown in the greenhouse were larger than those collected from the field populations, but all variables fell within the range of measurements observed in the field populations. This indicates that there is a genetic basis for the observed differences, and environmental conditions do not greatly effect the variables used to distinguish among the various taxa.

The potential for cotyledon characters in helping to distinguish species of *Leptosiphon* should be of interest to students of the genus. We noticed important patterns in our analysis of cotyledon width and length measurements. There were two basic cotyledon morphologies: long and linear, versus

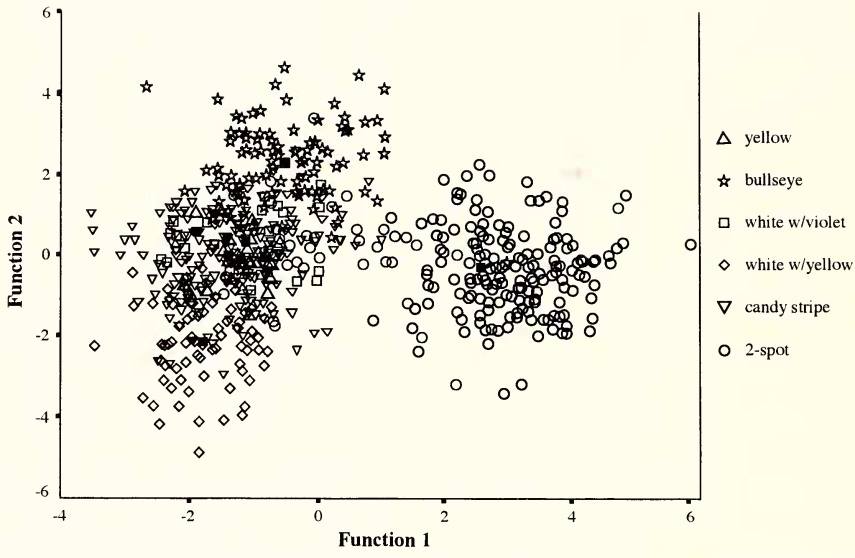

FIG. 7. Discriminant analysis from *L. parviflorus* color analysis (Matrix 3), all specimens (DA4-1). Graph of first two canonical functions for each individual.

shorter, rounded, and more or less obovate. The cotyledons of *L. acicularis* are linear and extremely long, with a length-to-width ratio of 7.1. *Leptosiphon parviflorus* also has linear cotyledons, with a ratio of 5.1; however two populations of *L. parviflorus* (LUC and JSP) had rounded cotyledons. These are each "2-spot" populations. The remaining species surveyed had oval to obovate cotyledons. *Leptosiphon androsaceus* had a length-to-width ratio of 1.8; *L. bicolor,* 1.9; *L. croceus,* 1.5, and *L. rosaceus,* 1.4. The length-to-width ratio of *L. latisectus* was 1.6.

The unidentifiable population, MRM, had cotyledons consistent with *L. androsaceus.* They were short and rounded, with a length-to-width ratio of 1.6. The cotyledons of the other unusual population, PNN, were longer and narrower than those of *L. bicolor* to which it was affiliated, with a ratio of 2.5, but they were not as linear as the cotyledons of *L. parviflorus.*

DISCUSSION

In closely related species that show far more similarities than differences, it is important to examine carefully all characters and to seek disjunctions among character states that may help define taxa and elucidate their relationships. Because the *L. androsaceus* group has a long taxonomic history accompanied by an abundance of nomenclatural activity, it is critical that we begin our analysis by examining morphological characters and identifying which of those best reflect relationships in the group. Despite the taxonomic age of the group, it has remained difficult to delineate species within it. Identification of taxa and the morphological characters that delimit them is a necessary precursor to further research on evolutionary relationships among these species. We focused on morphological characters because they are the most practical means of identification and without proper identification, further systematic research is compromised. Our results should be used as a working hypothesis of the taxonomic structure within the group, providing a framework for future research on evolutionary relationships among its species.

Results from our analysis support recognition of six species in central California (*L. acicularis, L. androsaceus, L. bicolor, L. parviflorus, L. croceus,* and *L. rosaceus*) bringing the number of species within the *L. androsaceus* complex to nine (including *L. latisectus* and *L. jepsonii* from northern California, and *L. serrulatus* from the southern Sierra Nevada). *Leptosiphon croceus* and *L. rosaceus* were described nearly 100 years ago, but were synonomized with *L. parviflorus* and *L. androsaceus* by later authors (Milliken 1904; Jepson 1925). Neither author offered any explanation for their action; however, the omission of these species may be explained by several factors, including the morphological similarity among all members of this complex, the large amount of variation observed in the few characters used for distinguishing them, and the relative rarity of both species. Each is known from only a few populations collected from coastal bluffs in the San Francisco Bay region. These bluffs have undergone severe disturbance from increased developmental activities in the last hundred years, and it is likely that of the populations of these species that were known, few remain. For example, *L. croceus* was originally described from a population near Pt. San Pedro, in San Mateo Co. In her description of the species, Eastwood (1904) observed

that "it covered the ground for several acres . . . the great masses almost monopolized the ground." Despite its historical presence, *L. croceus* no longer occurs in the Pt. San Pedro area. Today only one population of *L. croceus* is known.

In addition to the 6 species mentioned above, this study also identified 2 unusual populations. One relatively invariable population, from Pinnacles National Monument (PNN), consists of plants that most closely resemble *L. bicolor,* but its limb and stigmas are somewhat larger and the calyx shorter than typical *L. bicolor.* The coloration is also unusual, being light lavender (darker on the margins of the lobes fading to white near the throat) instead of the typical white or pink. This population is particularly interesting because *L. bicolor* is generally the least morphologically variable species in the *L. androsaceus* complex. In addition to the morphological similarity of PNN to *L. bicolor* evidenced by the multivariate analyses, the PNN plants grown in the greenhouse readily set seed, indicating it is autogamous. The only other plants to set seed in the greenhouse were from populations of *L. bicolor.*

The other unusual populations is the highly variable population from the Santa Cruz Mountains (MRM), a mosaic of *L. parviflorus* and *L. androsaceus.* Limb size was smaller than *L. androsaceus* and more like that of *L. parviflorus.* Flower color and limb lobe shape were like the white form of *L. androsaceus* (white lobes with a throat that is violet at the base and yellow above). Calyx pubescence is a stable character, yet the calyces from this population ranged from completely glabrous, to ciliate, to densely pubescent throughout, although never glandular. The within-population variance for most characters was high.

Morphological relationships among the L. androsaceus *complex in the Central and South Coast Ranges.*

Leptosiphon acicularis. This species is most clearly defined from others in this complex by the long, narrow, nearly needle-like leaf lobes. The size of the leaf palm is also the smallest in the complex, thus the leaves appear to be very finely dissected. The length of the calyx is long (7–9 mm), with the calyx lobes being narrow and much longer than the fused portion. *Leptosiphon acicularis* most closely resembles *L. bicolor,* both of which are the smallest-flowered members in this group. The limb of *L. acicularis* is always yellow, but the short corolla tube may be yellow or a light tannish pink (i.e., not always yellow as cited by Patterson [1993]). The shape of the tube is reminiscent of *L. parviflorus,* being very thin (0.5 mm), but in contrast to *L. parviflorus,* which may have extremely long tubes, the tube of *L. acicularis* is the shortest in the complex (11–17 mm). Although the limb of *L. bicolor* may also be light yellow, it is clearly distinguished from *L. acicularis* by a suite of other characters (calyx pubescence, shape of the leaf lobes, stigma length, stamen length).

Aside from its unique leaf morphology, *L. acicularis* also has a densely glandular pubescent calyx, whereas *L. bicolor* is pubescent only on the lobe margins and the trichomes are nonglandular. The size of the stamens and stigmas are also very different between the two species. *Leptosiphon acicularis* has some of the longer filaments in the complex (only those of *L. croceus* are as long), yet it has the one of the smallest limbs. Thus, the stamens of *L. acicularis* are well exserted, reaching ⅔ the length of the petal lobe. The stigmas are also large, being 2–4 mm long. The stamens of *L. bicolor* barely exceed the throat, and the stigmas are generally less than 1 mm long. As with most other species in this complex, the corollas open and close daily until senescence. The corollas of both species close for the night by mid-afternoon, earlier than the other species in the complex.

Leptosiphon androsaceus. This is the largest-flowered member of the *L. androsaceus* complex, and its floral characteristics most closely resemble *L. rosaceus* and *L. latisectus.* The limb lobes are the longest (8–11 mm) and differ from *L. rosaceus* and *L. latisectus* in being more oblong to oval, often with an apiculation at the tip. In comparison, the lobes of *L. rosaceus* and *L. latisectus* are very rounded. The limb is typically white or pale lavender, and the throat is commonly violet at the base, turning to yellow just as the throat flares into to limb. Buxton (1993) found populations in northern California with pink limbs, but none of the populations in this survey of central California had limbs with this color. The stigmas are generally long (2–4 mm) and the filaments are short in relation to the size of the limb. The corolla tube is typically moderate in length (19–26 mm), although this character is rather variable, and populations with longer tubes were observed. Similar to *L. rosaceus* and *L. latisectus,* the width of the tube is relatively wide (1 mm). Other characters differentiating this species include, leaf shape, plant height, calyx size, and most importantly calyx pubescence. The calyx is non-glandular and sparsely pubescent, with trichomes only on the margins of the lobes.

As with the other moderate- to short-tubed members, the total length of the calyx is moderately long (4–6 mm), with long calyx lobes relative to the fused portion. Nearly all leaf measurements for *L. androsaceus* are large for the complex. This species has the largest palm and longest middle lobe, although the width of the lobes is less than other species, giving it a less rounded appearance. The plants are typically the tallest growing members of the complex, and can occasionally be found growing on serpentine soil.

Grant (Grant and Grant 1965) observed a cyrtid fly, *Eulonchus smaragdinus,* visiting flowers of *L. androsaceus.* Although as a general rule he dis-

counted beetles as potential pollinators, we often observed beetles visiting flowers, probably not so much seeking out nectar as consuming pollen. Grant (Grant and Grant 1965) proposed *L. androsaceus* to be self-compatible and partially autogamous, with protandry being incomplete (overlapping stages). However, Goodwillie (1999b) showed it to be a self-incompatible, obligate outcrosser. Grant (Grant and Grant 1965) also suggested that *L. androsaceus* and *L. parviflorus* may hybridize locally, although he did not offer any evidence to support his statements. Hybridization is often invoked to explain unusual forms, but without careful study this explanation remains conjectural.

Leptosiphon bicolor. This species is morphologically the least variable member of the *L. androsaceus* complex. Its limb is small (3–4 mm), and its corolla tube is moderate in length (17–26 mm) and width (0.8 mm). It has by far the longest tube relative to the size of the limb. The limb is typically either pink or white with a yellow throat.

Its reproductive structures are small, with the stigmas 1 mm and stamens only one-half the length of the limb lobe, as might be expected in an autogamous species. The plants are relatively small (5–13 cm), and rarely is there more than one open flower per inflorescence. The flowers close by mid afternoon, opening again the following day.

The calyx is relatively long (7–9 mm), especially the length of the calyx lobes compared to the fused portion. The calyx is also ciliate and non-glandular, but, in contrast to *L. androsaceus* and *L. rosaceus,* the density of trichomes per lobe is generally greater in *L. bicolor* (30–50 trichomes per lobe). The leaves of *L. bicolor* are small, with short lobes and large palms. Buxton (1993) reported *L. bicolor* to have the greatest number of leaf lobes in the complex. In the southern populations, we found the variance of this character to be high both within and among populations, and we found no significant differences among the number of lobes in *L. bicolor, L. androsaceus, L. acicularis, L. parviflorus,* or *L. croceus.*

Goodwillie and Stiller (2001) recently elevated *Linanthus bicolor* (Nutt.) Greene subsp. *minimus* to species rank. While the scope of our study does not involve this species, following the taxonomy of Porter and Johnson (2000) the following combination is made:

Leptosiphon minimus (H. Mason) R. Battaglia, comb. nov. *Linanthus bicolor* var. *minimus* H. Mason. Madroño 9:249–255, 1948. *Linanthus minimus* Goodwillie and Stiller, Systematic Botany (2001). In press.

Leptosiphon croceus. First described by Eastwood (1904), *L. croceus* was later synonomized as varieties of *L. parviflorus* (Milliken 1904) and *L. androsaceus* (Jepson 1925). Our analysis supports its recognition as a distinct species. As with *L. latisectus, L. croceus* shares morphological characters with both *L. androsaceus* and *L. parviflorus* and many of the characters are intermediate between the two (e.g., limb size). Like *L. latisectus,* its leaf lobes are characteristically rounded at the tip, although its leaves are generally smaller. In addition, its leaves are thick and somewhat succulent. It is extremely low growing, being the shortest of all the species (2–6 cm). Although plants grown from seed of this population were slightly larger (6–8 cm) when raised in the greenhouse, they remained significantly shorter than any other species. Likewise, greenhouse grown plants also remained somewhat succulent, a likely response to conditions experienced directly on coastal bluffs. *Leptosiphon croceus* is often branched at the base with each branch having many closely spaced internodes. The close spacing of internodes makes the leaves appear "as if whorled" (Eastwood 1904). Its calyx is similar to that of *L. latisectus* in that the lobes and fused portion are nearly equal in length, and that it is densely glandular pubescent. The distinction lies in the size of the calyx and the width of the lobes.

Leptosiphon croceus has a much larger calyx (7–9 mm) than *L. latisectus,* and the width measurements are one-half to two times that of any other species. The limb is also similar in shape to that of *L. latisectus,* although the lobes are slightly larger (6–8 mm) and more rounded. The width of corolla lobes, both at middle and at the tip, are the largest in the complex. The corolla tube is also very long (29–37 mm), and thus distinguishes it from *L. latisectus.* The tube is generally much wider (0.9 mm) than that of *L. parviflorus,* more closely resembling *L. androsaceus* or *L. latisectus.* The limb is a bright, vibrant yellow, with an orange throat, and commonly has two red spots at the base of the lobes. The tube is yellow to yellowish-pink. In contrast to *L. latisectus,* the stigmas are relatively large (2–4 mm) and the filaments are long with the stamens exserted. The length of the filaments is similar to that of *L. acicularis.* Its cotyledons are rounded, like all the other species except *L. acicularis* and *L. parviflorus.*

Leptosiphon latisectus. This species has features of *L. androsaceus* and *L. parviflorus,* and closely resembles *L. croceus* in some features. As with *L. acicularis,* leaf measurements are important distinguishing characteristics. There are few leaf lobes, and they are wide at the tip, appearing more or less spatulate. Buxton (1993) showed palm lengths to be large, but variation in the two populations we sampled was too great to make conclusions. Its calyx is the smallest of any species in this group (5–7 mm). Its lobes are also small, nearly equal to the length of the fused portion. Its calyx is also densely glandular pubescent. Its limb shape and corolla tube width are similar to that of *L. croceus.* The limb lobes are moderate in size (5–7 mm), between *L. androsaceus* and *L. parviflorus,* but as with *L. croceus* they are especially wide at the tip, the lobes

being rounded to obovate. Unlike *L. croceus,* the tube is moderate in length (19–24 mm), similar to *L. androsaceus* and *L. bicolor.* The tube is also wide (≥ 1 mm) as is seen in *L. androsaceus* and *L. croceus.* A smaller limb with rounded lobes, a densely glandular calyx, and spatulate leaf lobes distinguish *L. latisectus* from *L. androsaceus,* while a comparatively larger limb, wider tube, and spatulate leaf lobes distinguish it from *L. parviflorus.* Corolla lobes are either dark pink or white, and the throat is yellow. The two pink populations sampled also had a white ring present at the top of the throat. Stigma length (1–2 mm) was among the smallest of any species (only *L. bicolor* had smaller stigmas), and filament length was short, barely exceeding the throat. Buxton (1993) suggested this might indicate possible autogamy, however Goodwillie (1999b) states *L. latisectus* is an obligate outcrosser. Individuals grown in the greenhouse had flowers that remained open even at night and in cooler temperatures, unlike any other species in the complex.

Leptosiphon rosaceus. This species was first recognized as *Leptosiphon parviflorus* var. *rosaceus* (Hooker 1870). Hooker considered this taxon a variety rather than a new species because he could find "no other difference" than the color and size of the flower (more than some authors would use). As to the flower, he stated it "was of a pale deep rose color, with a white or yellow eye" and that it "agrees with *L. androsaceus* one of the largest flowered of all," but that the lobes of the corolla had "a very different shape," being orbicular, versus narrower in *L. androsaceus* (Hooker 1870).

Greene (1889–1892) elevated Hooker's *Leptosiphon parviflorus* var. *rosaceus* to species level, *Linanthus rosaceus.* With regard to *L. rosaceus,* Greene observed that it was the "most beautiful plant of the *Leptosiphon* group" having stoutish short internodes, decumbent branches, obovate-spatulate leaf segments, the flower with a rose-red limb and an ample orange throat. He stated the "specific characters are as good as are found in this subgenus." He noted there was an albino form of this species as well. The population we observed during the course of this study was white. Another population discovered after the completion of the study was pink. Each of these observed populations had a yellow throat, not orange, as Greene described.

Occurring on coastal bluffs, its height and habit is similar to *L. croceus,* being densely branched and low growing (6–15 cm). It is significantly shorter than *L. androsaceus,* which is generally tall (17–31 cm) and not as densely branched. The leaf lobes of *L. rosaceus* are spatulate and more or less succulent. They are larger than those of *L. croceus* and even more rounded at the tip than either *L. croceus* or *L. latisectus.* The calyx is glabrous to sparsely pubescent, with the fewest number of trichomes per lobe than any other species in this complex (generally less than 10). If present, the trichomes are found only on the margins of the lobes and are nonglandular, another difference between it and both *L. latisectus* and *L. croceus.* The calyx lobes are moderately long (7–8 mm), but very wide at the base, appearing more or less deltoid.

The limb of *L. rosaceus* is moderate in size (7–9 mm) and similar in shape to *L. croceus* and *L. latisectus,* being smaller and more rounded than *L. androsaceus.* In contrast to *L. croceus,* the limb is white (or pink) with a pale yellow throat, and the corolla tube is not as long (21–26 mm). Tube length and width (1 mm) is more like that of *L. androsaceus* and *L. latisectus.* Unlike *L. androsaceus,* there is no violet coloration in the throat. The stigmas are generally long, being 4–5 mm, and well exserted beyond the throat.

Porter and Johnson (2000) did not include *L. rosaceus* in their recent revision; therefore the following new combination is made:

Leptosiphon rosaceus R. Battaglia, comb. nov. *Leptosiphon parviflorus* var. *rosaceus* Hooker. Curtis' Botanical Magazine 96, 1870. Tab 5863.

Leptosiphon parviflorus. Based on the analyses in this study *L. parviflorus* is taxonomically discrete at the species level, despite the observed variation. This species is variable in leaf and corolla size and shape, and especially so in corolla color pattern. In general, measurements for most morphological characters of *L. parviflorus* fell in the mid-range of the other species in the *L. androsaceus* complex (larger than *L. bicolor* or *L. acicularis,* smaller than *L. androsaceus* or *L. rosaceus*). The calyx is long (7–9 mm) and the calyx lobes are nearly equal in length to the fused portion. They are longer than *L. latisectus,* and not as wide as *L. croceus.* Like *L. latisectus* and *L. croceus,* an important identifying characteristic is its densely glandular pubescent calyx.

The limb lobes are 4–6 mm long and range from elliptic to oval or obovate. Lobe color may be white, pale yellow, yellow-orange, lavender-pink, or dark pink, with or without red spots or darker pink striations. The throat may be violet, yellow, or orange. In contrast to other species the throat is narrowly constricted at the base. Unlike *L. latisectus* or *L. croceus,* which have wider corolla tubes, the corolla tube of *L. parviflorus* is 0.6 (–1) mm, and 18–33 (–45) mm long. Tube length is highly variable, the standard deviation for tube length is twice that of the other species in this complex. Likewise, stigma length and style exsertion are also variable, as they lengthen over time in unfertilized flowers (Goodwillie 1999a). Stamens are well exserted, extending one-half the length of the corolla lobes. Goodwillie (1997) has shown *L. parviflorus* to be a self-incompatible, obligate outcrosser, with limited ability for wind pollination.

Corolla color patterns within L. parviflorus. Clearly different color patterns can be distinguished in this species, and some of these morphs correlate with other morphological features; however, the results of the multivariate analyses show distribution of these color patterns across *L. parviflorus* do not support sublevels of groupings. Within *L. parviflorus* the "2-spot" morph has the strongest support, and there is some weak support for the "bullseye" and "white with yellow" morphs based on the UPGMA clustering (Fig. 6) and the DA (Fig. 7), but examination of the variables fails to reveal distinct differences among the groups based on color.

Tube width and tube length are the characters responsible for the greatest separation between "2-spot" and the other color forms. The corolla tubes of the "2-spot" morph are generally very long (28–40 mm) and somewhat wider (0.8 mm) than those of the remaining color morphologies (0.5 mm). Tube length in the "bullseye" morph is also longer than average (22–29 mm), though not as long as the "2-spot," and, like the other color morphs, is much narrower (0.5 mm).

The limbs of "2-spot" and "bullseye" are also different, and provide a clearer separation than tube length. The "2-spot" color morphs have limb lobes that are larger than "bullseye" and are similar in shape to most other color morphs. In fact, all corolla measurements are consistently higher for the "2-spot" than the "bullseye" morphs. This is particularly true of the tip of the limb lobe, which is the largest in "2-spot" and the smallest in "bullseye." The limb lobes of "bullseye" are consequently narrower and more elliptic than the "2-spot," which are generally wider and more rounded, or flattened (Figure 2).

The differences between the "2-spot" and "bullseye" color morphs is interesting because these are the only color morphs with red markings on the corolla lobes. The presence of two red dots could seemingly evolve to become one large bar, or vice versa, and we would have expected their morphologies to be more similar. Also, the "2-spot" flowers have a yellow throat, whereas the "bullseye" have a dark yellow-orange throat.

Remaining Questions

Of the species in the *L. androsaceus* complex, *L. parviflorus* in particular raises many questions and merits further study. How is the variation in color pattern maintained? There is no geographic component to the color morphologies observed in our analysis, and only limited morphological separation. With such a highly modified corolla (nectar guides and long nectar tubes) and obligate outcrossing, it seems natural to expect specific pollinators are involved. Zebell (1993) examined a similar pattern of corolla color variation in *Calochortus venustus Benth.* He hypothesized that "flower color and pattern are 'released from tight pollinator selection pressures'. . . as long as enough flowers get pollinated to maintain the species." Perhaps the limited wind pollination in *L. parviflorus,* as reported by Goodwillie (1997), is enough of a selection release to allow for such variation in color morphology.

Based on the recent analytical work of Buxton (1993), Schemske and Goodwillie (1996), and Battaglia (1999), *L. parviflorus* should be approached with a careful eye. It is highly variable, not only in regard to color patterns, but in other vegetative and floral characters. Further taxonomic investigations, particularly populations of *L. parviflorus* from the Sierra Nevada foothills and south of the range covered in our analysis, are warranted to fully assess the variation observed in this species. Only after the fundamental morphological field work is completed to circumscribe the taxa can we begin to address other questions concerning phylogenies, population genetics, or the evolutionary history of the complex in California.

Taxonomic Key to the *Leptosiphon androsaceus* complex

1. Corolla tube <10 mm . . . . . *L. serrulatus*
1.′ Corolla tube >10 mm.
   2. Calyx densely pubescent throughout, trichomes glandular or non glandular.
      3. Leaf and calyx lobes acerose, corolla lobes generally <4 mm, corolla lobes yellow. . . . . *L. acicularis*
      3.′ Leaf and calyx lobes not acerose, corolla lobe color variable.
         4. Corolla lobes <3 mm, tube <14 mm, northern Puget Sound, Vancouver Island, possibly Coastal N CA . . . . . *L. minimus*
         4.′ Corolla lobes >3 mm.
            5. Calyx lobes deltoid, width at middle of lobe 1 mm, corolla lobes rounded at apex, always yellow, generally <7 cm tall, coastal bluffs San Mateo Co . . . . . *L. croceus*
            5.′ Calyx lobes narrowly acute, width at middle of lobe <1 mm, corolla lobes not both rounded at apex and yellow, generally >7 cm tall.
               6. Corolla tube width generally >1 mm, leaf lobes commonly spatulate, >2 mm wide, corolla lobes generally >6 mm and rounded . . . . . *L. latisectus*
               6.′ Corolla tube width generally <1 mm, leaf lobes not commonly spatulate, <2 mm wide, corolla lobe generally <6 mm and shape varied elliptic to obovate . . . . . *L. parviflorus*
   2.′ Calyx not densely pubescent, trichomes ciliate and non glandular.
      7. Corolla lobes <4 mm long, stigmas <1 mm . . . . . *L. bicolor*

7.′ Corolla lobes >4 m long, stigmas >1 mm
  8. Corolla lobes 4–6 mm long, stigmas generally <2 mm . . . . . *L. jepsonii*
  8.′ Corolla lobe 6–14 mm long, stigmas generally >2 mm
    9. Leaf lobes spatulate and more or less fleshy, corolla lobes generally 6–8 mm long and rounded, low growing, coastal San Francisco Bay area . . . . . *L. rosaceus*
    9.′ Leaf lobes not as above, corolla lobes generally >8 mm long, often with an apiculation at tip . . . . . *L. androsaceus*

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NOTEWORTHY COLLECTIONS

CALIFORNIA

CHORIZANTHE PARRYI VAR. *FERNANDINA* (POLYGONACEAE)—Ventura Co., S. slope of Laskey Mesa, Ahmanson Ranch; NE 3.2 Km Mureau Road and 101 Freeway, abandoned roadbed on compacted soils, San Andreas sandy loam, 1 May 1999, *R. E. Riefner & T. Bomkamp 99–271* (RSA); same location as above, 3 Jun 1999, *R. E. Riefner 99–283* (RSA); same location as above, 19 Jun 1999, *R. E. Riefner 99–299* (RSA).

Previous knowledge. Historically known from sandy places along drainages of the San Fernando Valley, northeastward into the Castaic Creek and Lake Elizabeth areas of the Liebre Mountains, and southward along the Los Angeles coastal plain into Orange County near Santa Ana (Reveal & Hardham 1989, Phytologia 66:98–198). Reveal and Hardham (loc. cit.) also report a J. G. Lemmon collection from San Bernardino County, but without other locality data, and several C. C. Parry collections without any locality information. Reveal and Hardham (loc. cit.) report 32 collections of the taxon, the most recent being Hoffmann's 1929 specimen from Elizabeth Lake. To this may be added an undated A. Davidson collection (s.n.) from Toluca (RSA 392509), and another A. Davidson specimen (s.n.) dated 11 May 1890 from Burbank (RSA 392787), both in Los Angeles County. These two specimens bear Reveal's annotation labels and were apparently omitted inadvertently from the 1989 paper.

Significance. Widely thought extinct (e.g., Skinner & Pavlik, C.N.P.S. Inventory of Rare and Endangered Vascular Plants of California, 5th ed., 1994; Hickman, ed., The Jepson Manual: Higher Plans of California, University of California Press, 1993; Reveal & Hardham loc. cit.). The type locality is San Fernando Canyon, Los Angeles County. The Laskey Mesa population represents a first record for Ventura County, and at present, the only known extant population. Seed collected from a number of the stands comprising the Laskey Mesa population have been placed into long-term storage at Rancho Santa Ana Botanic Garden (M. Wall, personal communication).

—STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.